RESEARCH REPORT

26

Development and Structure of Three High-elevation Old Spruce-Fir Stands in the Quesnel Highland of East-Central British Columbia

O.A. Steen, R.A. Coupé, H.M. Armleder, and R.J. Dawson

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BRITISH COLUMBIA

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ABSTRACT

This study describes the composition, size and age structure, and development of three old Engelmann spruce–subalpine fir stands at high elevations (>1500 m) in the Quesnel Highland in east-central British Columbia. The descriptions provide a basis for designing alternative silvicultural systems that will maintain usable old-forest habitat for mountain caribou and other old-growth–dependent species. Subalpine fir, which comprised 86% of all stems in the three stands, had inverse-J–shaped size and age profiles. Engelmann spruce included the largest trees in each stand but had bimodal size and age profiles. Age structure interpretations suggest that the stands have developed over periods of about 290–450 years since the last major stand-level disturbances (probably wildfires). Current stand age structures contain no clear evidence of post-establishment stand-level disturbances, although the data do not exclude the possibility of such disturbances. Approximately 29% of the fir trees and 13% of the spruce trees were dead. Age analyses of the tree seedling banks in the three stands indicate stable populations with continuous recruitment during the last 40 years. Young seedlings occurred preferentially on woody debris in advanced stages of decay, suggesting that seedling density differences among stands may be due at least partially to differences in the amount of woody debris.

The stand that apparently had the shortest time (about 290 years) for development since major disturbance had a structure that was still adjusting to disturbance. Evidence of this adjustment includes a bimodal fir age distribution and a high density of small trees that are apparently undergoing thinning. In addition, this stand had very few large (>60 cm dbh) live or dead trees and low volumes of coarse woody debris, especially in large and well-decomposed pieces, compared to the other two stands. A comparison of the three stands in this study suggests that naturally established high-elevation forests of the ESSFwc3 may not achieve some old-growth attributes, such as large dead trees and large, well-decomposed woody debris, until 400 or more years following initiation. The two stands in this study with the longest period of development (at least 450 years)

had balanced size and age structures and well-represented old-growth attributes such as large dead trees and large, well-decayed woody debris.

Planted stands may achieve some ESSFwc3 old-growth features several decades sooner than natural stands, due to a shorter stand initiation period. The alternative silvicultural system that has been proposed for maintaining suitable mountain caribou habitat following harvesting in this area (group selection system with 240-year rotation) will likely result in stands with many old-growth features, including abundant arboreal lichens. Some features that may not be present in these stands include a uniform inverse-J age distribution, many large (>60 cm dbh) live and standing dead trees, and large-diameter, well-decayed woody debris.

As old stands in the ESSFwc3 continue to age without outside disturbance, the spruce component of the stands will likely decline. Partial harvesting would help to maintain a significant component of spruce in these stands.

ACKNOWLEDGEMENTS

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INTRODUCTION

High-elevation old-growth Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)–subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests on the Quesnel Highland of east-central British Columbia are important winter habitat for mountain caribou (*Rangifer tarandus caribou* Gmelin) (Stevenson et al. 2001), a species that has recently been designated as nationally threatened (Caribou Strategy Committee 2000). In winter, caribou in this area depend on the abundant arboreal lichens found in old forests for food (Stevenson et al. 2001). Traditional timber harvesting practices, using clearcutting methods, remove the arboreal lichens from the harvest area and concentrate suitable old-forest habitat into increasingly smaller areas. Concentration of suitable habitat increases potential impacts of predation by wolves on the caribou population. Alternative silvicultural systems, using partial-harvesting methods, are being investigated to determine if timber can be harvested on a long-term basis while retaining sufficient old-forest attributes in harvested areas so that they remain as usable habitat for caribou and other old-growth–dependent species.

In order to manage for old-forest attributes in harvested areas, it is important to have descriptions of natural old stands that identify their attributes and development. Several authors have described the structure and dynamics of high-elevation old-growth spruce-fir stands of the central Rocky Mountains in the United States (e.g., Oosting and Reed 1952; Whipple and Dix 1979; Shea 1985; Alexander 1985, 1987; Veblen 1986; Aplet et al. 1988; Rebertus et al. 1992; Donnegan and Rebertus 1999; Binkley et al. 2003). Although the high-elevation spruce-fir forests of British Columbia share many floristic and environmental features with those of the central Rocky Mountains (Varga and Klinka 2001), climatic, geological, and other regional differences (Daubenmire 1943) suggest using caution in extrapolating results from the central Rocky Mountains to British Columbia (Feller 1997).

In western Canada, descriptions of the structure and dynamics of high-elevation old-growth spruce-fir forests are relatively recent (Day 1972; Jull 1990; Audet 1992; Parish 1997; Parish et al. 1999; Varga and Klinka 1996, 2001; Antos and Parish 2002a, 2002b; Parish and Antos 2002). In the interior of British

Columbia, high-elevation old-growth spruce-fir forests have been described by Parish (1997), Parish et al. (1999), Varga and Klinka (2001), Antos and Parish (2002a, 2002b), and Parish and Antos (2002). Although most stands are dominated by subalpine fir with variable amounts of Engelmann spruce, considerable variability of structure and dynamics appears to be present within the stands. Due to this variability, old-forest descriptions that can be applied to the study area should include information from stands within the study area. However, there are no available previous data on the structure and development of high-elevation spruce-fir stands within the Quesnel Highland. General ecological descriptions and ecological classifications of ESSF forests within or near the study area are given by Hamet-Ahti (1965), Annas and Coupé (1979), Thompson (1984), Coupé et al. (1991), and Steen and Coupé (1997), but these authors provide little information on stand structure or development.

The purpose of this study is to describe the composition, structure, and interpreted development of three old spruce-fir forests within mountain caribou winter range at high elevations (>1500 m) of the Engelmann Spruce–Subalpine Fir (ESSF) zone in the Quesnel Highland of east-central British Columbia. This study was initiated to provide guidance for planning and evaluating management practices to maintain old-forest features in managed stands at these elevations. The objectives of the study are to describe:

1. the composition and size structure of the stands as a reference for setting and evaluating stand structure goals,
2. the age structure of the stands as a basis for interpreting their origin and development,
3. the abundance of dead wood, including standing dead trees and woody debris, as a reference for deadwood management, and
4. the seedling bank as a basis for recommendations regarding the use of natural regeneration in managed spruce-fir forests of the study area.

The three old stands selected for this study are also being used for a broader study on the effects of group selection silvicultural systems on arboreal lichens, vegetation, hydrology, small mammals, birds, microenvironment, windthrow, and planted and natural regeneration of spruce and fir (Soneff and

Waterhouse 1997; Newsome et al. 2000a, 2000b; Stathers et al. 2001). Data for this and other pretreatment studies were collected during the summer of 1992, prior to harvesting during the following winter.

STUDY AREA

The three stands selected for this study are located in the Engelmann Spruce–Subalpine Fir Wet Cold subzone, Cariboo variant (ESSFwc3) (Steen and Coupé 1997) in the Quesnel Highland (Holland 1976), north and west of Quesnel Lake (Figure 1). Table 1 describes some environmental features of the sites.

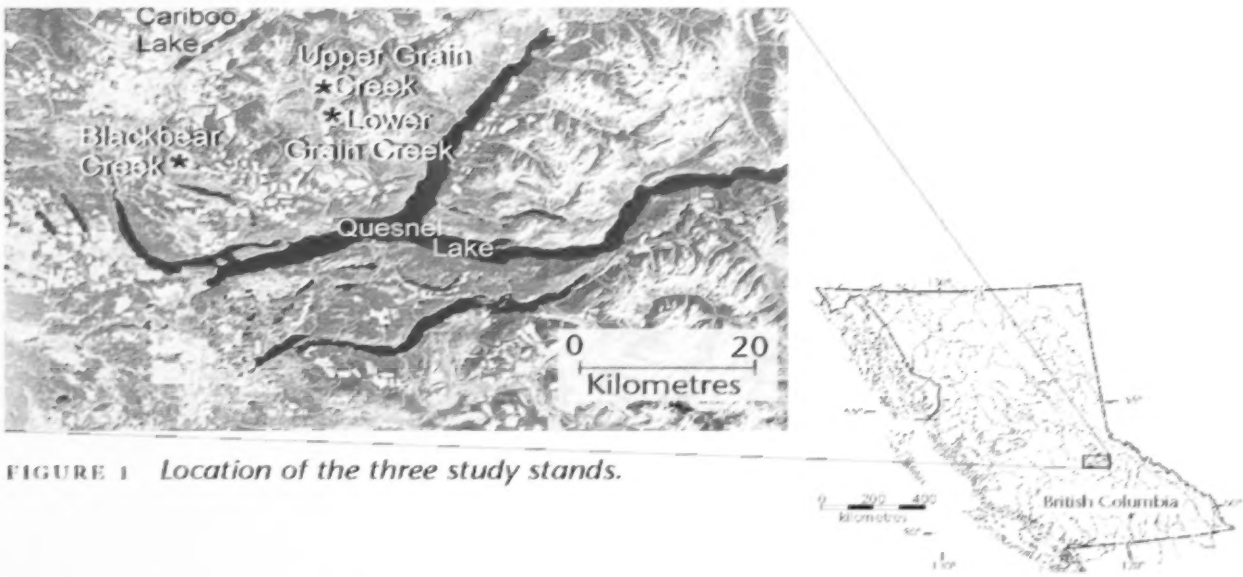

FIGURE 1 *Location of the three study stands.*

TABLE 1 *Environmental features of the three study sites*

Site	Location	Area (ha)	Elevation (m)	Slope (%)	Slope aspect
Blackbear Creek	52°36'37" N 121°24'30" W	61	1450–1590	15–40	northeast
Lower Grain Creek	52°40'45"N 121°10'52"W	40	1580–1700	15–35	northwest
Upper Grain Creek	52°41'29" N 121°12'02"W	41	1460–1640	20–25	west

The ESSFwc3 variant includes the highest-elevation forests of the Quesnel Highland and extends from approximately 1500 to 1800 m, where it borders alpine parkland or alpine tundra. The mature forests are dominated by subalpine fir and variable amounts of Engelmann spruce. Lodgepole pine is uncommon, and deciduous tree species are nearly absent. Early seral stands as well as mature and old stands are typically dominated by subalpine fir and spruce, although lodgepole pine is occasionally present on ridges and other relatively dry sites. Subalpine fir is the principal species in both the canopy and regeneration layers of old forests. Spruce is common in the upper canopy and seedling layers (Steen and Coupé 1997). The understory on mesic sites is dominated by a nearly closed, low shrub layer consisting primarily of white-flowered rhododendron (*Rhododendron albiflorum* Hook.), black huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.), and oval-leaved blueberry (*V. ovalifolium* Sm.). Common herbaceous species include five-leaved bramble (*Rubus pedatus* J.E. Sm.), rosy twistedstalk (*Streptopus lanceolatus* (Ait.) Reveal), Sitka valerian (*Valeriana sitchensis* Bong.), three-leaved foamflower (*Tiarella trifoliata* L.), and oak fern (*Gymnocarpium dryopteris* (L.) Newman) (Steen and Coupé 1997).

The climate of the ESSFwc3 variant is characterized by cold, snowy winters and cool, moist summers with approximately 1400 cm of precipitation annually and a mean annual temperature of -1.0°C (Farnden 1994; Steen and Coupé 1997). Peak snowpack is typically about 3 m, and snow is typically present on the ground from late October to mid June. Soils are typically loamy skeletal Humo-Ferric Podzols developed in glacial till. Soil humus forms on mesic sites are predominantly Hemimors (Green et al. 1993) less than 8 cm thick.

METHODS

Twenty-four to 26 plots were located at randomly selected points on a 50 × 50 m grid within each of the three stands. Each plot was inspected in the field to confirm that it had a predominantly mesic soil moisture regime (Luttmerding et al. 1990) and was generally representative of the stand structure. In some cases, plot locations were offset by a pre-planned distance and bearing

to avoid wet microsites and other non-representative areas.

Each plot included a main plot and a nested subplot. The main plot was established to record all stems ≥7.5 cm dbh (diameter at breast height [1.3 m]) and was most often 200 m^2 (r = 7.98 m). In areas with a high density of stems, plot size was reduced to 100 m^2 (r = 5.64 m). The main plot was also used to describe shrub and herbaceous vegetation. A 50-m^2 subplot (r = 3.99 m) was established within each main plot to record all stems <7.5 cm dbh, including germinants less than 1 year old. However, in subplots with a very large number of small seedlings, only stems >0.3 m tall were recorded in the subplot, and smaller stems were sampled in four 4-m^2 microplots (r = 1.12 m) systematically located with their centres 3 m from the main plot centre in each of the four cardinal directions.

In the main plot, all stems with a dbh ≥7.5 cm were identified to species, measured for dbh, total height, and condition, and cored at 0.3 m height for aging. In approximately 15% of stems, a core was taken from a height of 1.3 m due to decay at lower heights. In these cases, estimated age was later adjusted for coring height based on comparisons of ages at 0.3 m and 1.3 m in a few subcanopy stems. It is recognized that these generalized corrections are likely inaccurate for some stems, but the implications of the inaccuracies are considered minor to the overall conclusions of the study. In a few cases, a sound core could not be obtained at either level from a tree, so 30 cm–height ages were later estimated from diameters based on age/diameter regression equations developed for the site. The number of trees from which a sound core could not be obtained was small. All cores were returned to the laboratory for counting of annual rings.

Tree condition was described as live or dead, and by wildlife tree class (Wildlife Tree Committee of British Columbia 1993), integrity of bark, and characteristics of the upper crown. Bark integrity was described as intact, loose, partially missing, or entirely missing. The upper crown was described as live, dead, or missing.

Each stem in the main plot was also identified as part of a tree clump or as an isolated individual. A tree clump was defined as a group of stems in which crowns of adjacent trees were separated by less than one crown width and stems were isolated from stems outside the clump by more than two crown widths. In most cases, tree clumps were easily recognized. For each identified clump, the number of stems ≥7.5 cm dbh in the clump

and the dimensions of the clump were recorded. Dimensions were recorded as the lengths of the long axis and the axis perpendicular to the long axis.

In the nested subplots and microplots, each stem <7.5 cm dbh was identified to species, and its basal (ground-level) diameter, height, condition, age, and type of substrate and microrelief on which it grew were recorded. Basal diameter was measured with a caliper to the nearest millimetre. Height was measured with a clinometer, height pole, metre stick, or 15-cm rule, depending upon the size of the stem. Condition was recorded simply as live or dead. Age was determined from a cross-section of the stem cut at ground level by counting annual rings with a hand lens in the field or returning the section to the laboratory for counting under a binocular microscope. Substrate was considered to be surface materials at the juncture of the stem and the surface, and was recorded as decaying wood, humus form, exposed mineral soil, fractured rock, or tree root. Decaying wood substrate was further described in terms of decay classes 1–5 (Maser et al. 1988), and humus substrate was described as ≤10 cm or >10 cm. Microrelief at the base of the stem was described as raised, level, or depressed and by height of the relief above or below the immediately adjacent surface. Height was estimated relative to surfaces within 2 m of the base of the stem by laying an imaginary straight edge on the general surface and estimating height to the nearest 2 cm above or below this surface. The percentage of each subplot surface covered by coarse (≥10.0 cm diameter) woody debris, humus form, exposed mineral soil, and rock was visually estimated.

Age estimates based on ring counts at ground level in shade-tolerant species such as subalpine fir have been noted as potentially inaccurate by several authors (Kneeshaw and Claveau 2001; Wong and Lertzman 2001; Parent and Morin 2002; Parent et al. 2002; Peters et al. 2002). These potential inaccuracies are of significant concern if sufficient accuracy is required to correlate ages of individual stems to independent temporal data (Wong and Lertzman 2001). Potential inaccuracies are of less concern when the objective, as in this study, is to describe general age structure of the population, especially when age classes are broad.

Coarse woody debris volumes on the three sites were estimated by the line intercept method. Lines were initiated at

randomly selected points and extended for 75 or 100 m along randomly selected bearings. Small openings within the sites were avoided. Each piece of woody debris 10 cm in diameter or larger was identified to species if possible and measured for diameter and decay class (Maser et al. 1988). Volumes (m^3/ha) were calculated by size class, decay class, and all size and decay classes combined.

The percentage of ground cover for each shrub, herb, and terrestrial moss and lichen species within the main plot was visually estimated. The total combined cover of tall (≥2 m) shrubs, low (<2 m) shrubs, herbs, and bryophytes/lichens was also visually estimated.

RESULTS

TREE SPECIES COMPOSITION

Subalpine fir and Engelmann spruce were the only common tree species in the three stands. A few stems of lodgepole pine were present on two of the 73 plots, and a single small stem of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) occurred on one plot.

Subalpine fir was the dominant species in all three stands. On average, 86% of all stems were fir, with a nearly equal representation between stems ≥12.5 cm dbh and those that were smaller. In the three stands, the fir proportion of all stems ranged from 81% at the Blackbear Creek site to 83% at the Upper Grain Creek site and 91% at the Lower Grain Creek site. However, the largest trees in all three stands were primarily spruce. For example, spruce was more abundant than fir in the upper third of the stand dbh range at all three sites (>45 cm at the Blackbear Creek site and >58 cm at the Lower Grain Creek and Upper Grain Creek sites) (Table 2). As a result, the basal area of fir trees ≥12.5 cm dbh in the three stands averaged only 71% of total tree stand basal area with a range of 70–73% in the three stands. The Blackbear Creek stand had the highest density and basal area of stems ≥12.5 cm dbh but the lowest density of smaller stems (Table 2).

TABLE 2 *Tree species composition of the three study stands*

	Stems/ha						Basal area (m^2/ha) ≥ 12.5 cm dbh	
	<12.5 cm dbh		≥ 12.5 cm dbh		Upper 1/3 of diameter range			
Stand	Bl	Se	Bl	Se	Bl	Se	Bl	Se
Blackbear Creek	4 250	1 020	632	104	4	42	40	16
Lower Grain Creek	28 675	2 864	372	45	4	29	28	12
Upper Grain Creek	34 795	6 922	317	40	11	26	29	11
Mean	22 573	3 602	440	63	7	31	32	13

SIZE STRUCTURE

The three stands each contained a full spectrum of tree heights, resulting in deep multi-layered forest canopies and understories. Subalpine fir height profiles had an inverse-J shape in all three stands, especially in the Lower and Upper Grain Creek stands (Figures 2 and 3). The decrease in fir stem density with increasing height in the Blackbear Creek stand was less consistent than at the other two sites, but no tree canopy layers were clearly evident (Figure 4).

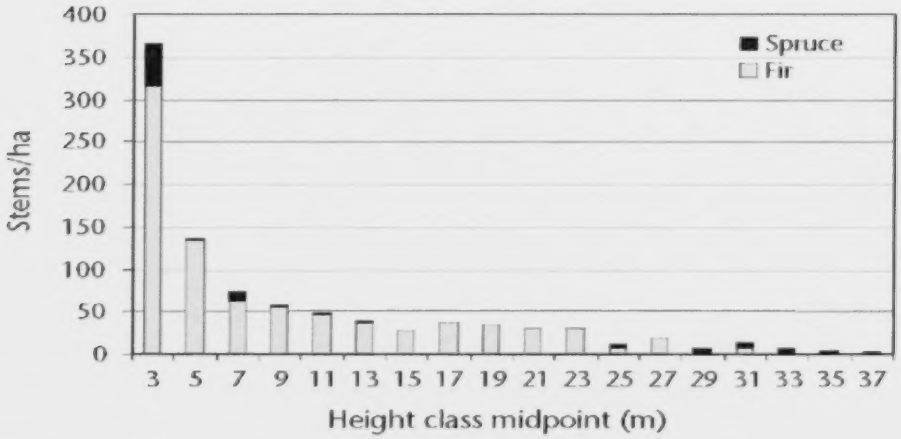

FIGURE 2 *Live tree height structure (2-m classes) of the Lower Grain Creek stand. The 0–2 m height class is not shown due to its very large number of stems (28 217 fir and 2812 spruce/ha).*

In contrast to subalpine fir, spruce had a bimodal height distribution, with several stems in the upper canopy 24–40 m tall and several stems in the lower regeneration layer <4 m tall. Only a small number of spruce stems occurred in intermediate height classes. The tallest trees at each site were spruce, with maximum heights of 38–42 m. Fir was also present in the upper canopy with maximum heights of 32–36 m.

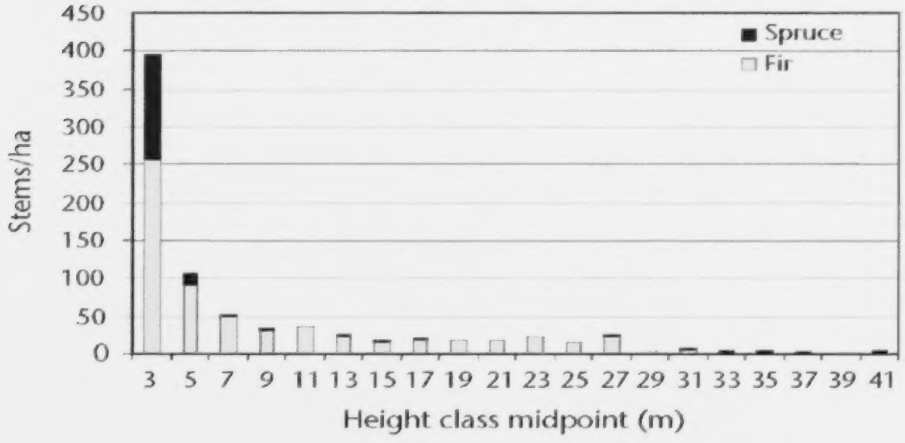

FIGURE 3 *Live tree height structure (2-m classes) of the Upper Grain Creek stand. The 0–2 m height class is not shown due to its very large number of stems (36 068 fir and 7087 spruce/ha).*

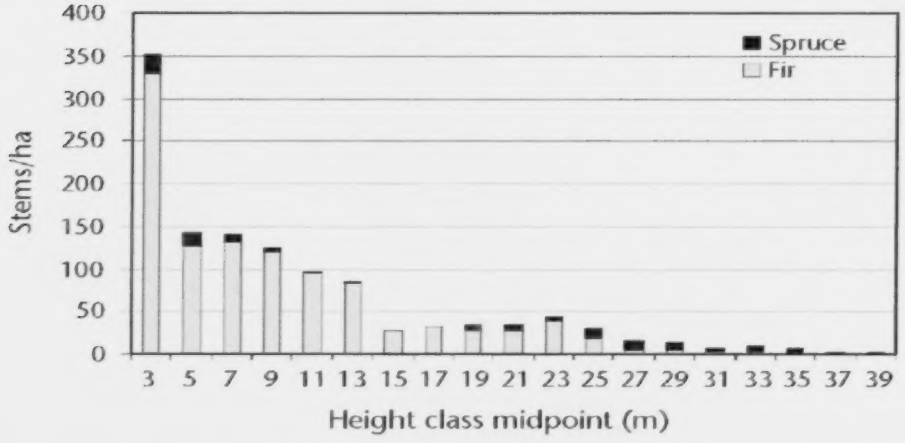

FIGURE 4 *Live tree height structure (2-m classes) of the Blackbear Creek stand. The 0–2 m height class is not shown due to its very large number of stems (3141 fir and 958 spruce/ha).*

Stem diameter (dbh) class frequencies at the three stands were similar to the height profiles. Fir had an inverse-J–shaped distribution, while spruce had a bimodal distribution with several stems in the upper and lower parts of the dbh range but few in the intermediate size classes (Figures 5, 6, and 7).

A comparison of stem diameter profiles at the three sites shows that the Blackbear Creek stand had fewer large-diameter trees (>60 cm dbh) than either of the two Grain Creek stands, but a relatively large number of small trees (7.5–17.5 cm dbh). For example, the Blackbear Creek stand had only eight trees/ha >60 cm dbh while the Lower and Upper Grain Creek stands had 35 and 27 trees/ha, respectively. In contrast, the Blackbear Creek stand had 2–3 times as many stems 7.5–17.5 cm dbh as the Lower and Upper Grain Creek stands (403 vs 204 and 136 stems/ha, respectively). The larger total basal area of the Blackbear Creek stand (Table 2) is due to a greater number of small trees, not the presence of large trees.

AGE STRUCTURE

Age class profiles of the three stands help to interpret the height and diameter profiles and further demonstrate differences between the Blackbear Creek stand and the two Grain Creek stands. Fir had an inverse-J distribution, with trees in all age classes except the oldest. However, as for size, the age class distribution of spruce was bimodal, with trees in the oldest and youngest age classes but few in the intermediate age classes (Figures 8, 9, and 10). The bimodal age profiles of spruce suggests that, in contrast to fir, spruce regeneration is not commonly recruited to the forest canopy in undisturbed stands and does not appear to commonly survive more than about 80 years under a canopy.

The presence of several old spruce trees in a wide range of age classes in the canopy of each stand (Figures 8, 9, and 10) suggests that conditions affecting spruce establishment and growth have changed since these trees were established. In particular, forest canopy and shrub layers were likely more open when the trees were recruited to the canopy and they are most likely remnants of a cohort that developed following a disturbance that partially or completely removed the previous forest canopy. Based on the ages of the oldest spruce trees in each

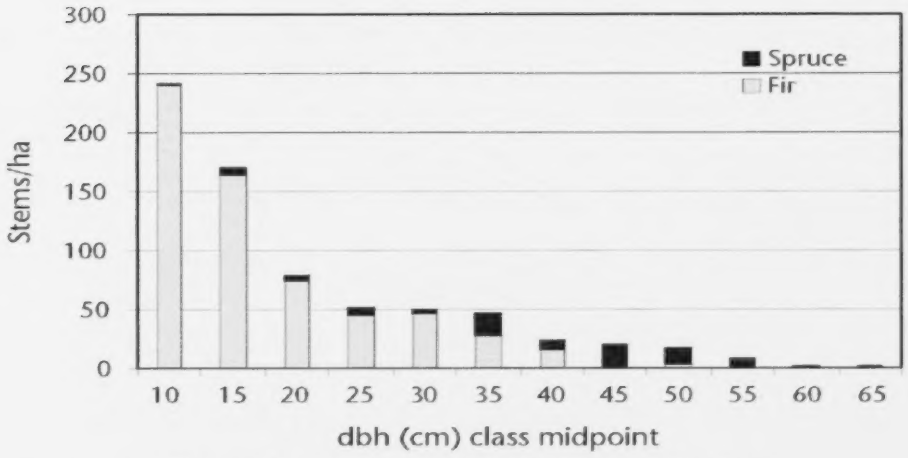

FIGURE 5 *Stem diameter (cm dbh) structure of live trees ≥7.5 cm dbh in the Blackbear Creek stand.*

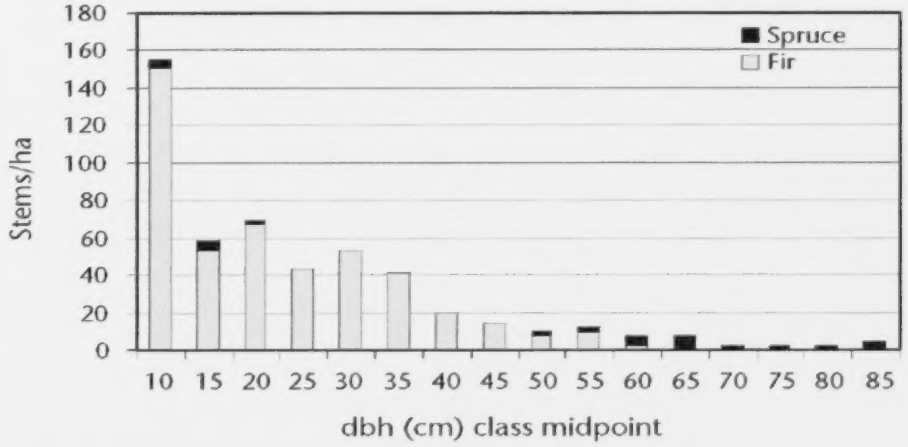

FIGURE 6 *Stem diameter (cm dbh) structure of live trees ≥7.5 cm dbh in the Lower Grain Creek stand.*

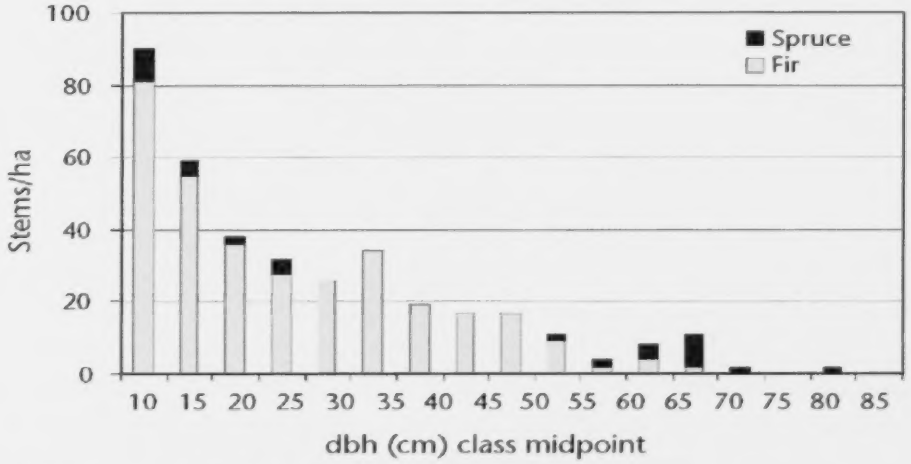

FIGURE 7 *Stem diameter (cm dbh) structure of live trees ≥7.5 cm dbh in the Upper Grain Creek stand.*

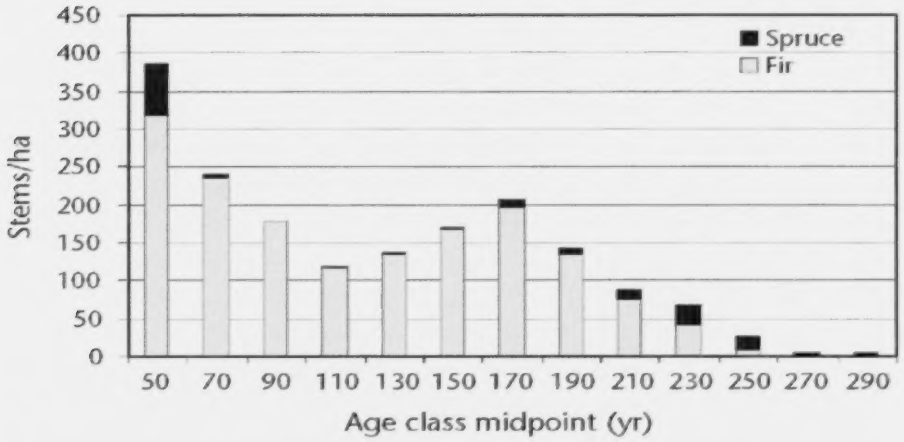

FIGURE 8 *Live tree age structure of the Blackbear Creek stand (20-year age classes). See Figure 17 for density of stems <40 years old.*

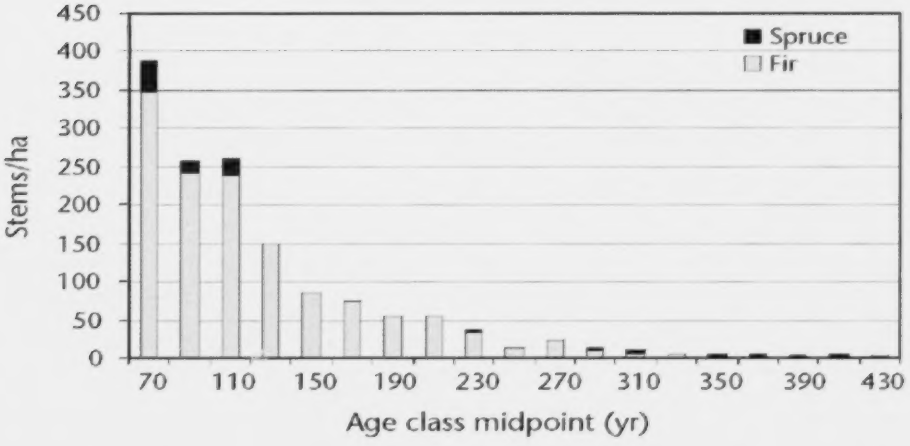

FIGURE 9 *Live tree age structure of the Lower Grain Creek stand (20-year age classes). See Figure 17 for density of stems <60 years old.*

stand, this disturbance likely occurred about 450 years ago at the Upper Grain Creek and Lower Grain Creek sites and about 290 years ago at the Blackbear Creek site.

The small number of trees >60 cm dbh in the Blackbear Creek stand compared to the Lower and Upper Grain Creek stands (Figs. 5, 6, and 7) probably reflects the fact that few trees >250 years old were present in the stand. Although spruce commonly reaches diameters >60 cm, most spruce ≥60 cm dbh in the three stands were >250 years old (Figure 11). The Blackbear

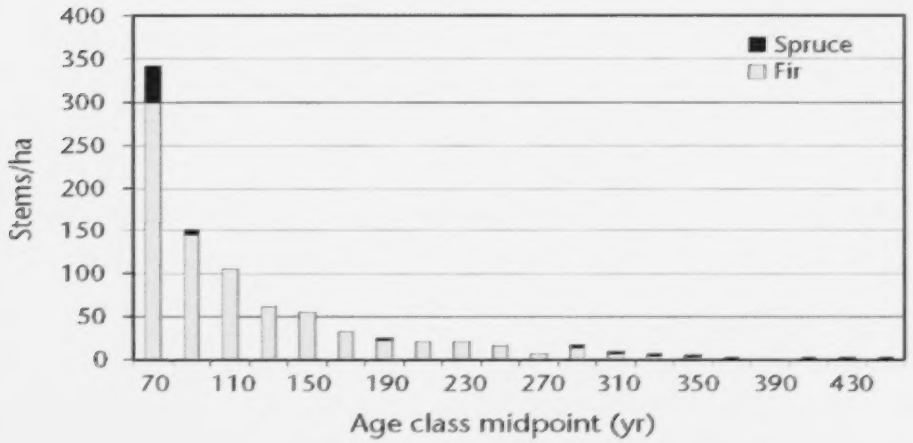

FIGURE 10 *Live tree age structure of the Upper Grain Creek stand (20-year age classes). See Figure 17 for density of stems <60 years old.*

Creek stand, which has likely been developing for <300 years since major disturbance, may not be old enough to contain more spruce of this size.

In the Blackbear Creek stand, spruce achieved a greater total height than fir (Figures 12 and 13), and the mean height of both species increased up to the oldest age class without an indication of a maximum mean height. No plateau or height asymptote was evident. In the Lower Grain Creek stand, however, fir mean height in 20-year age classes increased to a maximum of about 25 m, while spruce mean height increased to a maximum of about 35 m (Figures 14 and 15). Both species reached their maximum mean height at about 250 years, beyond which mean height was relatively constant. Potential maximum tree height at the Blackbear Creek site may be greater than at the Grain Creek sites due to its lower elevation.

The oldest fir and spruce trees recorded in the Blackbear Creek, Lower Grain Creek, and Upper Grain Creek stands were 242 and 297 years, 422 and 446 years, and 372 and 426 years, respectively.

TREE CLUMPS

Field observations in high-elevation ESSFwc3 forests indicate that trees very commonly occur in clumps. Clumping was noted especially in the Lower and Upper Grain Creek stands but was

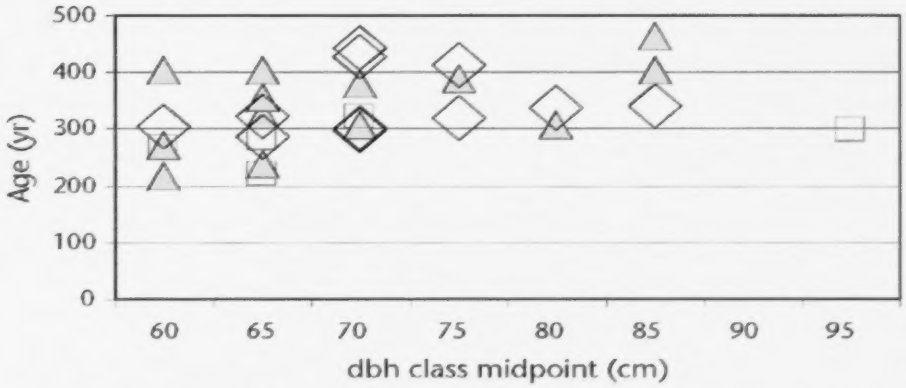

FIGURE 11 *Age of spruce trees ≥57.5 cm dbh. Stands in which the trees occurred is indicated by the symbol: □ = Blackbear Creek, △ = Lower Grain Creek, ◇ = Upper Grain Creek.*

FIGURE 12 *Mean height of subalpine fir stems in 20-year age classes in the Blackbear Creek stand. Vertical bars are ±1 S.E. of the mean.*

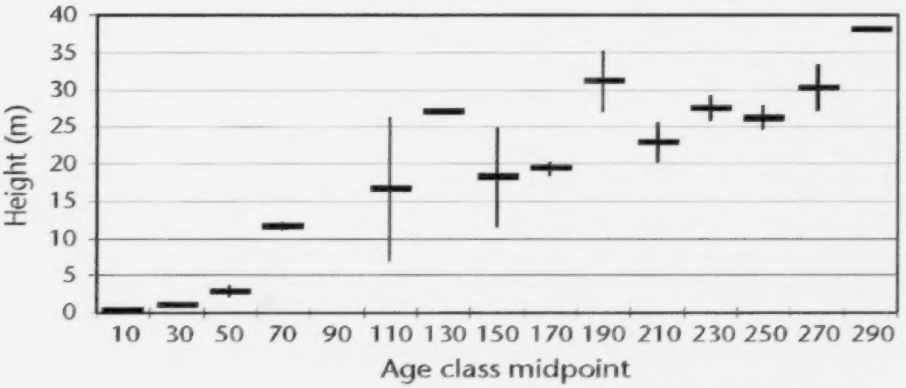

FIGURE 13 *Mean height of spruce stems in 20-year age classes in the Blackbear Creek stand. Vertical bars are ±1 S.E. of the mean.*

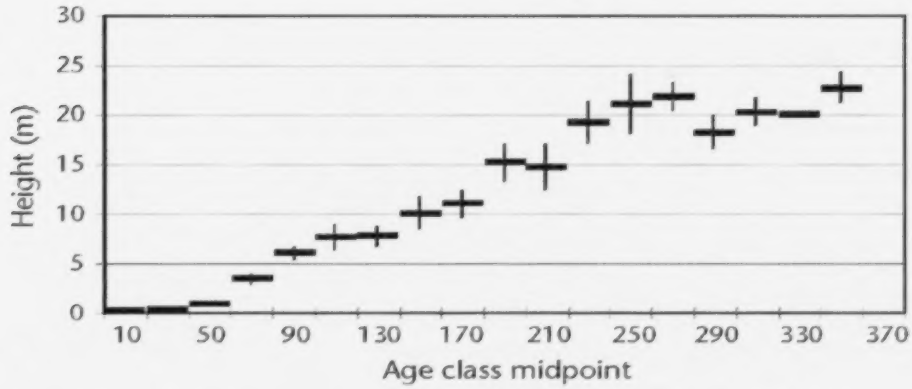

FIGURE 14 *Mean height of subalpine fir stems in 20-year age classes in the Lower Grain Creek stand. Vertical bars are ±1 S.E. of the mean.*

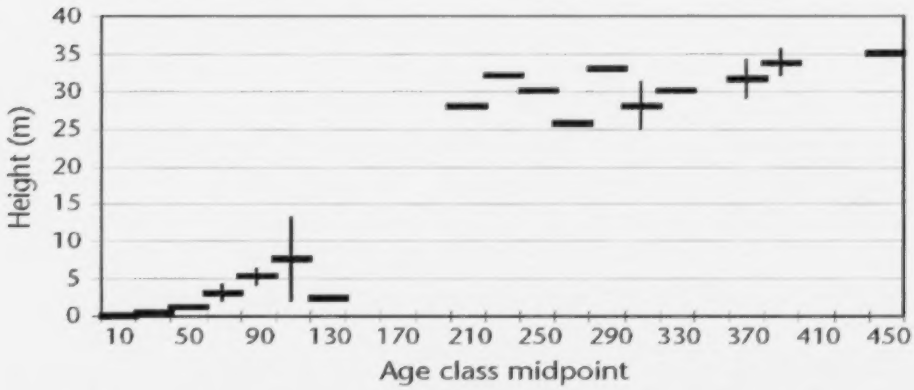

FIGURE 15 *Mean height of spruce stems in 20-year age classes in the Lower Grain Creek stand. Vertical bars are ±1 S.E. of the mean.*

somewhat less evident in the Blackbear Creek stand. Although no detailed assessment of spatial pattern was done, 83 and 86% of the stems ≥7.5 cm dbh were identified as part of a clump in the Lower Grain Creek and Upper Grain Creek plots, respectively. In the Blackbear Creek plots, 65% of the stems ≥7.5 cm dbh were identified as part of a clump. The mean area of clumps was 24–25 m^2 in the two Grain Creek stands and 29 m^2 in the Blackbear Creek stand. The mean number of trees per clump was 4.1, 4.3, and 6.5 in the Upper Grain Creek, Lower Grain Creek, and Blackbear Creek stands, respectively.

Dead trees are a characteristic feature of these old, high-elevation forests. Over the three stands, dead trees comprised an average of 22% of the total standing volume, including 25% of the fir volume and 15% of the spruce volume. An average of 29% of the fir trees and 13% of the spruce trees were dead. The Blackbear Creek stand contained a much higher proportion (40%) of dead fir trees than did either the Lower Grain Creek stand (21%) or the Upper Grain Creek stand (16%).

Standing dead spruce trees occurred primarily in intermediate size classes. Although spruce mortality is probably very high in the population of stems <2.5 cm dbh, few very small dead stems were evident. Dead fir trees were most numerous in the small diameter classes in the Blackbear Creek stand and in intermediate to large diameter classes in the two Grain Creek stands (Figure 16). Although cause of mortality was not determined in this study, it is likely that many of the fir trees, especially those in the larger diameter classes, were killed by endemic levels of western balsam bark beetle and the lesion-causing fungus (*Ceratocystis dryocoetidis*) it introduces into the stem.

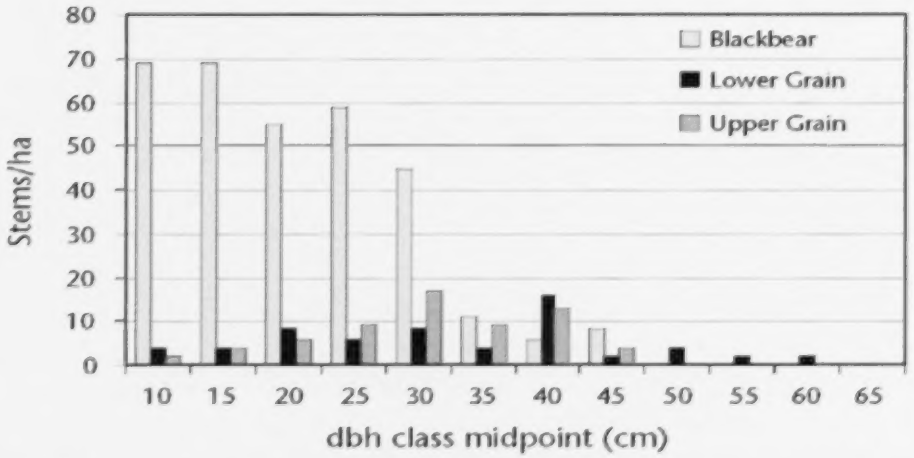

FIGURE 16 *Stem diameter (cm dbh) class structure of standing dead trees ≥7.5 cm dbh in the three stands.*

COARSE WOODY DEBRIS

Volumes of coarse (>10.0 cm diameter) woody debris ranged from 149 m^3/ha on the Blackbear Creek site to 322 m^3/ha on the Upper Grain Creek site (Table 3). The lower volume on the Blackbear Creek site is due primarily to the relatively small size of woody debris on this site. Only about 40% (59 m^3/ha) of the total volume on the Blackbear Creek site was in pieces >27.5 cm in diameter. In contrast, 91% (231 m^3/ha) and 86% (277 m^3/ha) of the total volume on the Lower and Upper Grain Creek sites, respectively, was in pieces >27.5 cm in diameter. Woody debris >45 cm in diameter was not recorded on the Blackbear Creek site but was common on the two Grain Creek sites. These differences are consistent with differences between the three stands in size structure of dead and live trees.

In addition, volumes of woody debris in medium and advanced stages of decay (decay classes 3–5) were 2–2.5 times greater on the Grain Creek sites than on the Blackbear Creek site (Table 3). Volumes in less advanced stages of decay (decay classes 1 and 2) were similar on all three sites.

TABLE 3 *Volume (m^3/ha) of coarse (≥10.0 cm diameter) woody debris by decay class (Maser et al. 1988)*

	Decay class					
Stand	1	2	3	4	5	Total
Blackbear Creek	6	39	63	30	11	149
Lower Grain Creek	0	45	115	56	39	255
Upper Grain Creek	4	47	125	130	16	322

SHRUB AND HERBACEOUS VEGETATION

The three stands had similar shrub and herbaceous vegetation (Table 4). A very well developed shrub layer, 1–1.75 m tall, covered half or more of the surface in each of the stands.

TABLE 4 *Mean and standard deviation of percentage cover of shrub and herb vegetation strata*

	Vegetation stratum			
	Tall (>2 m) shrubs	Low (≤2 m) shrubs	Herbs	Bryophytes and lichens
Blackbear Creek	6 (7)	59 (22)	34 (16)	42 (21)
Lower Grain Creek	5 (5)	44 (16)	42 (22)	53 (15)
Upper Grain Creek	3 (2)	60 (22)	41 (17)	39 (16)

This dense shrub layer was dominated by white-flowered rhododendron (*Rhododendron albiflorum* Hook.) and included smaller amounts of black huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.) and oval-leaved blueberry (*V. ovalifolium* Sm.). Herbaceous plants covered one-third to one-half of the surface and were mostly less than 15 cm tall. Principal species were Sitka valerian (*Valeriana sitchensis* Bong.), oak fern (*Gymnocarpium dryopteris* (L.) Newman), mountain arnica (*Arnica latifolia* Bong.), rosy twisted-stalk (*Streptopus lanceolatus* (Ait.) Reveal), three-leaved foamflower (*Tiarella trifoliata* L.), and five-leaved bramble (*Rubus pedatus* J. E. Sm.). Bryophytes covered about half of the surface at each site, and principal species were *Rhytidiopsis robusta* (Hedw.) Broth. and species of *Brachythecium, Mnium, Dicranum,* and *Barbilophozia.* In contrast to lower-elevation ESSF sites, boreal feathermosses (*Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.), and *Hylocomium splendens* (Hedw.) B.S.G.) were uncommon, and the moss mat was thin (≤1.5 cm).

TREE SEEDLING BANK

As is generally characteristic of old forests in the ESSFwc3, tree seedlings were abundant in the three stands, which contained, on average, about 24 000 stems/ha of fir and spruce <2.5 cm dbh. Although no quantitative data were collected on distribution of these stems, observations indicate that they were concentrated at the base of larger trees and at the periphery of tree clumps. This distribution pattern may be due to the longer snow-free

period and warmer microclimate near the larger trees.

In the three stands, stems <2.5 cm dbh originated primarily from seed but 4–8% of the fir and 0–3% of the spruce originated by layering (Table 5). Layering was most common in the Upper Grain Creek stand.

The density of very small (<2.5 cm dbh) fir and spruce stems in the Blackbear Creek stand was only 10–12% of the densities in the Lower and Upper Grain Creek stands (Table 5). Similarly, the density of <20-year-old stems in the Blackbear Creek stand was <10% of densities in either the Lower or Upper Grain Creek stand (Figure 17). In contrast, the Blackbear Creek stand had greater densities of stems 7.5–12.5 cm dbh than did the two Grain Creek stands (Figures 5, 6, and 7). This pattern was also

TABLE 5 *Density (stems/ha) of stems <2.5 cm dbh originated from seed and by layering.*

	Fir		Spruce	
	Seedling	Layered	Seedling	Layered
Blackbear Creek	3 116	153	980	0
Lower Grain Creek	26 721	1 036	2 736	17
Upper Grain Creek	32 592	2 703	6 767	205

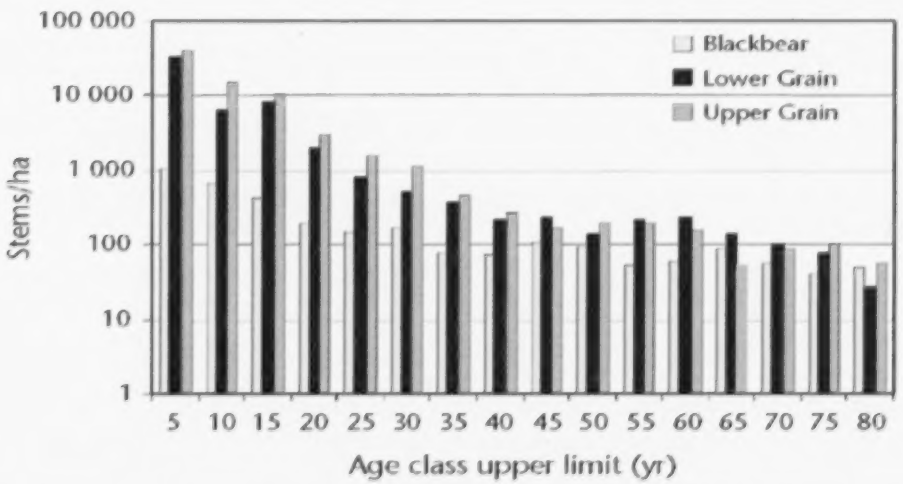

FIGURE 17 *Age structure (5-year age classes) of live fir stems ≤80 years old in the three stands.*

evident in the age structure of very young stems at the three sites (Figure 17).

Age structure of live fir stems up to 80 years old (Figure 17) indicates that the higher densities of young and small stems on the two Grain Creek sites are not due to a recent pulse of seedling establishment. Five-year age class frequencies at all three sites show a relatively uniform, exponential decrease in stem density up to 40 years of age without any apparent anomalies. This suggests stable populations with continuous recruitment at all sites during the last 40 years.

Regeneration density differences between the three sites can be at least partially explained by seedbed differences, especially the amount of coarse woody debris. Most young fir seedlings in the three stands occurred on decaying woody debris (Figure 18). Although coarse woody debris formed less than 15% of the surface materials (on an area basis) at each site, 50 to nearly 90% of the fir seedlings <20 years old occurred on woody debris. In contrast, humus form layers covered nearly 90% of the surface at the three sites but supported only 15–20% of the fir seedlings <20 years old. Exposed mineral soil was very uncommon (<1% cover), but where it was present as a result of root tip-ups, etc., it usually supported small spruce and fir seedlings.

The proportion of very young (<20 years old) fir seedlings on coarse woody debris increased with the stage of decay of the debris. Seedling concentration, calculated as the proportion of seedlings occurring on a decay class divided by the proportion

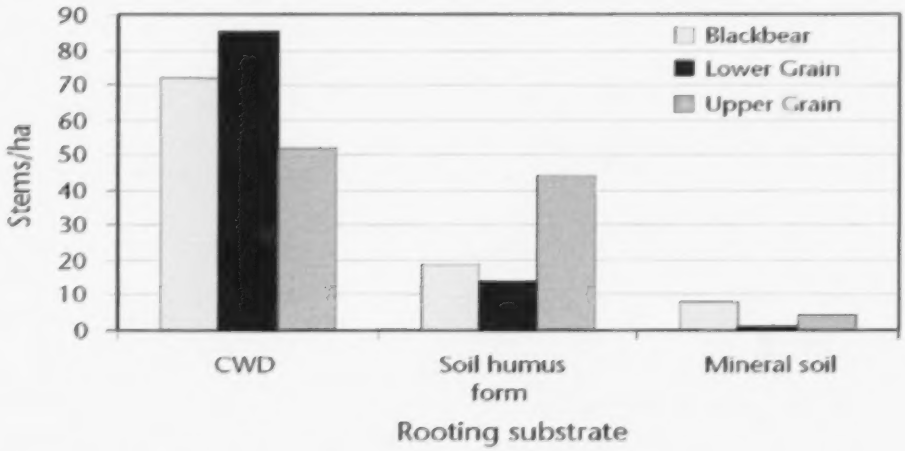

FIGURE 18 *Density of fir stems ≤20 years old on coarse woody debris (CWD), soil humus form, and exposed mineral soil.*

of total woody debris volume in that decay class, increased consistently with increasing decay class at all three sites (Figure 19). Note that basing the concentration calculation on volume underestimates the increase in concentration per decay class based on unit of surface area. Although no quantitative data are available regarding distribution by size class, observations indicated that young seedlings were also more common on large than on small pieces of woody debris. The large pieces provide greater microtopographic relief and probably more stable thermal and moisture conditions.

Raised microsites generally supported the greatest proportion of seedlings (Figures 20 and 21). At the Blackbear Creek site, 73% of the fir and 93% of the spruce were on raised microsites. At the Upper Grain Creek site, 80% of the fir and 74% of the spruce were on raised microsites. Raised microsites were often formed by woody debris.

Given the apparent importance of coarse woody debris to the seedling bank, the large differences in young seedling densities among the three sites may be partially due to difference in the volume, size, and decay class of woody debris. Both Grain Creek sites had greater total volumes, larger piece sizes, and

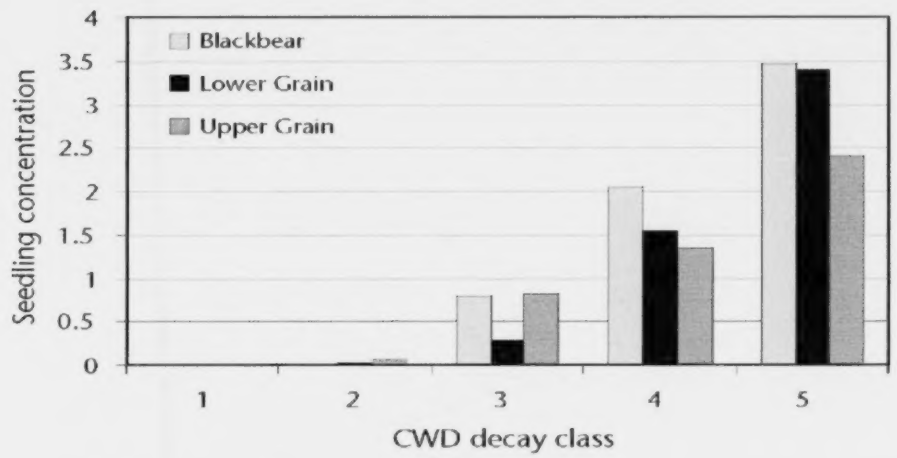

FIGURE 19 *Concentration of fir seedlings ≤20 years old on coarse woody debris decay classes. Concentration is the proportion of all seedlings occurring on a CWD decay class divided by the proportion of total CWD volume in that decay class.*

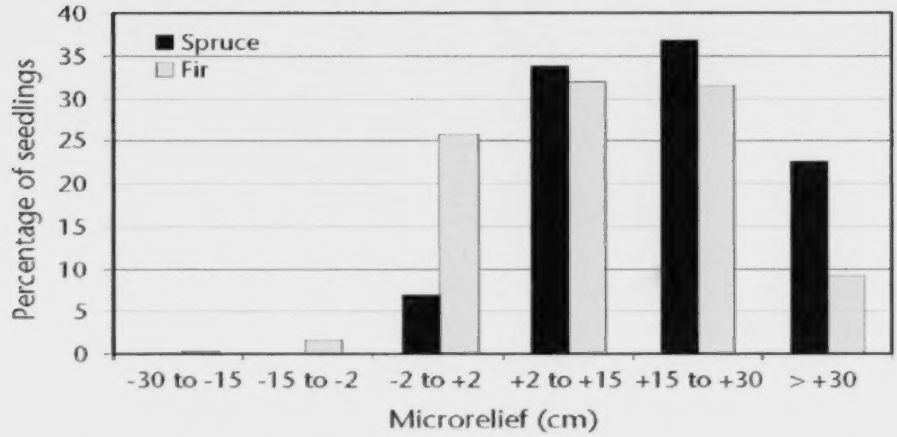

FIGURE 20 *Percentage of seedlings on classes of microrelief above or below the adjacent surface in the Blackbear Creek stand.*

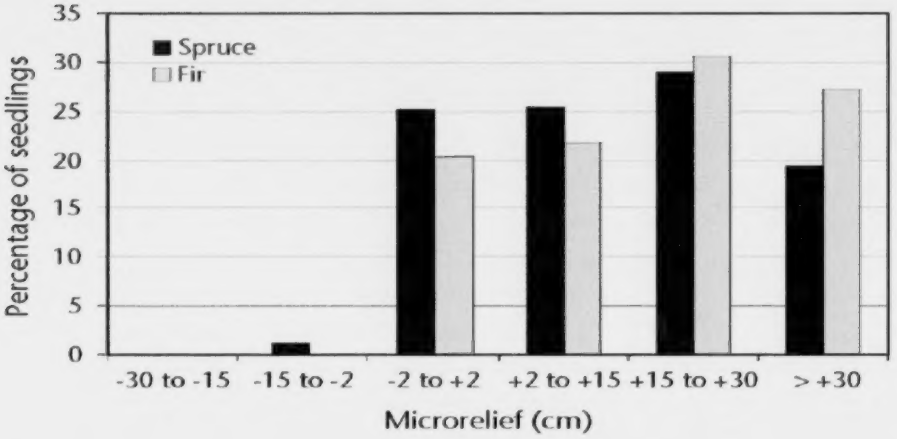

FIGURE 21 *Percentage of seedlings on classes of microrelief above or below the adjacent surface in the Upper Grain Creek stand.*

greater volumes in decay classes 3–5 than did the Blackbear Creek site (Table 3).

Differences in seedling densities between sites cannot be explained solely by differences in coarse woody debris, however, since density differences were also evident on humus form substrates. The Blackbear Creek site had 452 fir stems/ha <20 years old on humus form compared to 10 580 and 3875 stems/ha in the Lower Grain Creek and Upper Grain Creek sites, respectively. Similarly, the Blackbear Creek site had only 38 spruce stems/ha <20 years old on humus form substrates com-

pared to 651 and 828 stems/ha on the Lower Grain Creek and Upper Grain Creek sites, respectively. Different densities on humus form substrates were apparently not due to different thicknesses of humus form layers, which averaged 3.7, 4.4, and 2.7 cm on mesic microsites at the Blackbear Creek, Lower Grain Creek, and Upper Grain Creek sites, respectively.

Since shrub and herbaceous vegetation was similar at the three sites (Table 4), it also does not account for seedling density differences. However, the Blackbear Creek stand had a more closed tree canopy, as indicated by higher tree basal area and density, than either of the two Grain Creek stands (Table 2). The more closed tree canopy, in combination with low amounts of coarse woody debris, likely limited tree seedling establishment in the Blackbear Creek stand compared to the two Grain Creek stands.

If the age structure of the seedling bank in the two Grain Creek stands is stable (as suggested by Figure 17), then the very large numbers of seedlings <20 years old in these stands is apparently balanced by high rates of mortality. Table 6 shows the ratio of seedling numbers in a 20-year age class and the previous 20-year age class. These ratios suggest that the rate of seedling survival from the 0- to 19-year age class to the 61- to 79-year age class is much lower in the two Grain Creek stands than in the Blackbear Creek stand. As expected, the steepest decline (lowest survival rate) in seedling numbers is from the first to the second age class at all three sites. The apparently high rate of seedling mortality in the two Grain Creek stands may be important to the persistence of their open forest canopy.

TABLE 6 *Ratios between stem densities in one 20-year age class and a younger 20-year age class*

	Age class comparison			
	2 vs 1	3 vs 2	4 vs 3	4 vs 1
Blackbear Creek	0.20	0.59	0.64	0.08
Lower Grain Creek	0.08	0.43	0.37	0.01
Upper Grain Creek	0.12	0.21	0.40	0.01

DISCUSSION AND MANAGEMENT IMPLICATIONS

Tree species composition of the three study stands was similar to that in other high-elevation old-growth spruce-fir stands that have been described in British Columbia (Parish et al. 1999; Varga and Klinka 2001; Antos and Parish 2002a, 2002b). Engelmann spruce proportions were similar to those in areas further south in British Columbia (Parish et al. 1999; Antos and Parish 2002a) but slightly more abundant than those reported in west-central British Columbia, northwest of the study area (Varga and Klinka 2001). The representation of lodgepole pine in the study stands is less than that reported for old-growth spruce-fir forests of southwestern Alberta (Day 1972), while the representation of spruce is less than that reported for many high-elevation spruce-fir forests in the central Rocky Mountains (Oosting and Reed 1952; Whipple and Dix 1979; Aplet et al. 1988).

Varga and Klinka (2001) suggest that height growth of understory fir stems in high-elevation spruce-fir stands is cyclic, with periods of suppressed growth followed by periods of faster growth when several canopy stems die. Although growth release was not assessed in this study, the stands were not layered.

Each of the three stands had an inverse-J age distribution of fir (slightly bimodal in Blackbear Creek stand) but a strongly bimodal distribution of spruce, with stems in the oldest and youngest age classes. Although spruce seedlings were common, spruce saplings and small trees were rare, suggesting that very few of the seedlings in undisturbed old stands survive long enough to form subcanopy or canopy stems. Although there are many dead trees in these stands, the scattered mortality of subcanopy and canopy stems is apparently insufficient to allow common spruce recruitment to the canopy.

The presence of several large, old spruce trees in the upper canopy of the three stands and the absence of apparent spruce recruitment to the canopy suggests that conditions for spruce establishment and growth have changed since the old canopy stems were established. That is, these stems most likely developed following a stand-level disturbance that partially or completely removed the previous forest canopy.

It is most likely that the disturbance that allowed development of these spruce stems was a stand-level disturbance that

affected most of the previous canopy and low shrub layer as well as the forest floor. This interpretation is based on spruce regeneration patterns in the existing stands. The forest canopies of the Lower and Upper Grain Creek stands are quite open, with tree vertical projections typically covering no more than 25% of the surface, and with many gaps of more than four to five crown widths between trees. Beneath the open canopy, the forest floor is covered by a dense shrub layer 1.0–1.75 m tall. In spite of the open forest canopy and presence of young spruce seedlings, there is little or no apparent spruce recruitment into the canopy of the stands. In addition, large seedlings or saplings of spruce are seldom present around fallen large trees unless tree fall resulted in mineral soil exposure.

If the old spruce trees in the canopy of these stands are remnants of a cohort that established following a major stand disturbance, the ages of the oldest stems in each stand implies that this disturbance occurred about 450 years ago at the Upper Grain Creek and Lower Grain Creek sites and about 290 years ago at the Blackbear Creek site.

An alternative interpretation is that the stands have been present for a longer period of time and the canopy spruce stems are remnants of stems that established beneath an existing canopy or following partial canopy disturbance events (such as mortality due to epidemic levels of western balsam bark beetle). Although this interpretation cannot be ruled out by existing data, it is considered much less likely than the previous interpretation, based on the current regeneration patterns.

Western balsam bark beetle and the associated lesion-causing fungus *Ceratocystis dryocoetidis* have been suggested as the cause of extensive canopy mortality and the resulting peaks of regeneration and growth release in spruce-fir stands of southern British Columbia (Parish 1997; Parish et al. 1999). Although this pest most often kills <5% of trees distributed throughout a stand within a year, it occasionally kills high numbers of trees in a single season (Garbutt 1992; Henigman et al. 2001). Endemic-level attacks are likely responsible for the high proportion of the dead fir trees in the stands studied, but there is no evidence of a post-establishment stand-level disturbance episode in the age profiles of the two Grain Creek stands. In these stands, fir has a uniform age profile and spruce shows no post-establishment peaks in age or size class representation, except in the youngest age classes.

In the Blackbear Creek stand, fir has a bimodal age distribution, with the older peak starting about 80–100 years after the oldest stem. One possible explanation of this peak is that it represents fir regeneration that established as the result of a partial stand-level disturbance event (such as epidemic attack by western balsam bark beetle). This interpretation is consistent with results from other ESSF stands in British Columbia (Parish 1997; Parish et al. 1999). However, the peak occurs only in the fir age distribution and is not evident in the spruce population. The absence of a spruce establishment response may be the result of partial canopy disturbance without disturbance to the shrub layers or forest floor. In this case, the only spruce response may have been growth release of existing stems without establishment of a new cohort. No radial growth data were available to examine this possibility. Another consideration is that the fir peak occurs at the end of the spruce establishment phase, when canopy trees were mostly <100 years old and probably of small to moderate size. Although possible, a western balsam bark beetle epidemic is unlikely in such a stand since this insect attacks mostly moderate-size to large trees (Henigman et al. 2001). Other disturbance events such as extensive snowpress or windthrow are also possible.

Although the fir age peak may be the result of a partial disturbance after stand initiation, it is considered more likely that the peak is the result of normal stand development following a stand-initiating disturbance. That is, the peak may reflect the change from a stand initiation phase (sensu Oliver and Larson 1996) age distribution to a stem exclusion phase age distribution. In this interpretation, abundant fir regeneration ingress and high survival rates occurred during the stand initiation period, when the tree canopy and possibly shrub layers were open and tree seedling growth was not density dependent. As growth of established fir and spruce seedlings began to close the canopy and fully occupy the site, subsequent establishment and survival of fir decreased. Spruce establishment and survival appears to have essentially ceased when fir establishment reached its peak. Aplet et al. (1988) refer to the cessation of spruce establishment during spruce-fir stand development as the spruce exclusion phase, similar to the stem exclusion phase described by Oliver and Larsen (1996) but applying more to spruce than to fir.

The three stands of this study were not all at the same stage of stand development. The two Grain Creek stands, which are

estimated to have been initiated 460–480 years ago, have a relatively uniform age distribution of fir, relatively high numbers of trees that have apparently reached their maximum height for these environments, stem mortality that is distributed throughout size classes, and abundant woody debris in a wide range of size and decay classes, including large-diameter and well-decomposed pieces. In contrast, the Blackbear Creek stand, which was likely initiated about 290 years ago, had a slightly bimodal fir age structure, few spruce stems that have reached their maximum height for the site, high mortality of small (<30 cm dbh) stems (suggesting a trend for increasing concentration of stand basal area in large stems), relatively low seedling densities (suggesting stem exclusion by a closed canopy), and relatively low volumes of woody debris, with comparatively little representation of large or well-decomposed pieces.

The 300 years that the two Grain Creek stands have been developing since the beginning of the stem exclusion stage is apparently sufficient for these stands to contain few residual stems from the initiation stage, a characteristic of old-growth stands (Oliver and Larsen 1996; Varga and Klinka 1996; Kneeshaw and Burton 1998), and to achieve other characteristics of old-growth spruce-fir stands in the ESSFwc3. However, the approximately 170 years that the Blackbear Creek stand may have been developing since the end of the initiation phase has not resulted in the same old-growth characteristics.

The Forest Practices Code of British Columbia classifies stands >250 years old in the ESSFwc3 as old seral stage. However, our interpretation of the development of the Blackbear Creek stand suggests that stands of natural origin in the ESSFwc3 variant <400 years old may not yet have all attributes characteristic of old-growth forests, such as many large trees for the site, large dead trees, and large, well-decomposed woody debris. That is, like the Blackbear Creek stand, they may still be undergoing structural development. As old-growth reserves are lost through stand-destroying events, replacements must be found or recruited to beyond 400 years old before they fully function as old-growth forests.

Unpublished data collected from three stands in the ESSFwc3 on Mount Tom, about 80 km northeast of the study area, support this conclusion. The youngest of the three stands, which had no trees older than 272 years, had features of a stand still undergoing structural development following a stand-initiating

disturbance. These features included a high proportion of stand basal area in small trees, a high number of dead trees mostly in small to medium size classes, and low volumes of coarse woody debris (C. Gabriel, pers. comm.[1]). Varga and Klinka (1996) analyzed subalpine fir stem diameter distributions in nine large plots within old ESSF stands in west-central British Columbia. They concluded that the stands ≥300 years old had not yet achieved a balanced diameter distribution, as indicated by fit to a negative exponential model. The distributions still showed evidence of the initial colonizing cohort.

1 C. Gabriel.2004. Structure of three high-elevation Engelmann spruce – subalpine fir stands on Mt. Tom, British Columbia Unpublished Biology Co-op Program Work Term Report, Univ. Victoria, Victoria, B.C.

Stands established through plantations of spruce and fir may develop some attributes that are characteristic of old-growth forests sooner than the naturally established stands in this study, since planting likely shortens the stand initiation phase, moving the stand more quickly into the stem exclusion phase (as characterized by Oliver and Larson 1996). Attributes that will likely develop sooner in planted stands include stable size structures and relatively high proportions of stand basal area in large trees. However, attributes that may not develop within 250 years in many planted stands include uniform negative exponential age distributions, large numbers of trees of maximum size for the site, large standing dead trees, and an abundance of large, well-decomposed woody debris.

While the Blackbear Creek stand differed from the older (greater time since initiation) Grain Creek stands in several ways, the older stands do not have more arboreal forage lichen (M. Waterhouse and H. Armleder, pers. comm.[2]). Larger trees are more common in the older stands, but large spruce are typically devoid of lichen-bearing branches on the lower bole, where caribou feed. Conversely, a clumpy tree distribution, as noted in the older stands, can favour arboreal lichens (Campbell and Coxson 2001). From the standpoint of caribou winter forage, it appears that there is no net advantage to stands older than 300 years in the Quesnel Highland study area.

2 B.C. Ministry of Forests, Southern Interior Forest Region, Williams Lake, B.C., unpublished data.

The long-term fate of spruce in the two Grain Creek stands, as they continue to age without major disturbance, is unclear. Spruce will continue to be present, as evidenced by abundant young regeneration in current stands, as long as a seed source is available. However, the number of spruce trees in the upper canopy will likely continue to decline, since there are few intermediate-size stems for recruitment to the upper canopy. Localized mortality of individual trees or small groups of trees results in

increased growth of subcanopy stems to fill the gap created by canopy mortality (Lertzman and Krebs 1991; Lertzman 1992). Shea (1985) argues that this mechanism will maintain a spruce component within subalpine old-growth stands in Colorado. However, due to the dense cover of low shrubs and the great abundance of fir stems in the subcanopy of ESSFwc3 stands, spruce establishment and survival would likely continue to be suppressed in the canopy gaps. A larger stand-level disturbance, resulting in mortality of several canopy and subcanopy fir stems, as well as reduced cover of low shrubs, will likely be required to maintain current spruce representation in the upper canopy. A western balsam bark beetle outbreak, such as described in southern British Columbia (Parish 1997; Parish et al. 1999), could provide such a disturbance to the canopy but not to the dense shrub layer. In addition, such an outbreak may not be sufficiently frequent or widespread to prevent long-term decline in the number of spruce in the upper canopy. Alternatively, stand- and patch-initiating disturbances such as wildfire and timber harvesting should re-establish the long-term role of spruce in the canopy.

The three study stands, and especially the two Grain Creek stands, had quite open canopies, often with loose clumps of trees separated by small, treeless openings with no dead canopy stems and little or no tree regeneration. These openings do not represent a stage in a gap dynamics process initiated by a gap-maker (Lertzman and Krebs 1991) but rather are likely related to microsite physical and biotic factors. They may be considered "edaphic gaps" (Lertzman et al. 1996). In the vicinity of these openings, tree regeneration was most abundant at the periphery of small clumps of trees, similar to the distribution reported by Audet (1992) and Varga and Klinka (1996). Brett and Klinka (1998) and Varga and Klinka (2001) suggest that this regeneration pattern reflects the transition from gap-phase to tree-island regeneration models, with the latter becoming more significant at higher elevations.

The development of these three stands, as interpreted here, has several implications for the group selection silvicultural system that is proposed for maintaining mountain caribou winter habitat values of these high-elevation spruce-fir stands. The proposed system includes harvesting one-third of the stand area in small patches or groups of trees (0.2–1.0 ha) every 80 years. The time between harvesting of an individual patch will be

approximately 240 years. Assuming that the stand-initiation phase on the individual openings may require only 40 years (due to artificial regeneration), then an additional 200 years will be available for stand development prior to the next harvest of an individual patch. This is slightly longer than the period of stand development following the stand-initiation stage at Blackbear Creek but shorter than the period at either of the two current Grain Creek stands. As a result, stand development on the individual patches can be expected to be at least as advanced as the Blackbear Creek stand but less developed than the two current Grain Creek stands.

In particular, the managed stands should continue to have a significant component of spruce in the canopy due to frequent harvesting disturbances. However, unless mature spruce trees are reserved at each cutting cycle, maximum spruce size will likely be smaller than that in the current Grain Creek stands and possibly smaller than that in the current Blackbear Creek stand. Very few (if any) trees will be >250 years old. In addition, standing dead trees will likely be mostly small to medium-sized, as in the Blackbear Creek stand, and recruitment of coarse woody debris will be mostly small to medium-sized stems.

Management practices can enhance old-growth attributes of partially harvested high-elevation stands. Reserving mature windfirm spruce trees within or near the edge of group selection openings at each harvest entry would maintain a component of larger spruce trees in the managed stand. These larger trees would also provide a long-term source of large woody debris, which may otherwise be poorly represented in the managed stands.

A wide range of woody debris sizes and stages of decay can also be left on-site following harvesting. In addition to providing valuable habitat, this debris should ensure that the spruce and fir seedling bank (advance regeneration) is present for at least the first cycle of harvesting. This may be particularly important if a goal is to use advance regeneration to complement planting or natural regeneration ingress. Several studies have shown that spruce and fir regeneration under a forest canopy occurs predominantly on decaying wood (Day 1964; Knapp and Smith 1982; Harvey et al. 1987). The greater abundance of regeneration on woody debris than on the soil humus form layer may be due, at least in part, to seed and seedling pathogens associated with the humus form (Zhong and van der Kamp 1999).

As noted in this study, exposed mineral soil will likely increase spruce establishment. However, since spruce growth is apparently reduced on mineral soil compared to undisturbed forest floor (Feller 1998), small mineral soil patches may result in more vigorous spruce regeneration than would large patches.

Clumpy tree distribution, an attribute of high-elevation old spruce-fir forests that favours arboreal lichen growth (Campbell and Coxson 2001), can be enhanced by plantations with a clumpy distribution of planted seedlings.

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